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Phylogenetic and Biogeographic Aspects of *Sophora* Sect. *Edwardsia* (Papilionaceae)[1]

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ABSTRACT: *Sophora* comprises 45–50 species of worldwide distribution, but no general proposal as to the evolution of this group has been put forth. We used cladistic relationships of the quinolizidine alkaloids (matrine, sparteine, methylcytisine, anagyrine, and sophoranol) with morphological and palynological characters to suggest a hypothesis of evolutionary and biogeographic relationships. The mainland Chilean species of *Sophora* appear to have been derived from ancestors phylogenetically near the extant Argentinean species *S. linearifolia* and *S. rhynchocarpa* and the psammophyte *S. tomentosa,* growing at tropical coastal sites around the world. The Boreotropic hypothesis of Lavin and Luckow is incorporated in our model as the most parsimonious explanation of the evolution of the species of *Edwardsia. Sophora* is a taxonomic group that meets the following criteria: a center of diversity in North America, an early Tertiary record in North America, and a pantropical distribution. *Styphnolobium* and *Sophora* (including *Calia*) are representatives of *Sophora* s.l. in the United States, suggesting a migration of the latter from the Northern Hemisphere to South America. Consistent with the Boreotropic hypothesis, a primary diversification center in South America and subsequent migration to the Indian Ocean and New Zealand, the Juan Fernández Archipelago, Easter Island, and possibly the Hawaiian Islands is the simplest explanation for the evolution of the *Edwardsia* species.

Valid species of *Sophora* following revisions of Allan (1961), Yakovlev (1967), Green (1970), Godley (1979), Isely (1981), Tsoong and Ma (1981), and Heenan (1998) are listed in Table 1. Although Tsoong and Ma (1981) merged *Calia* and *Styphnolobium,* it is better to consider them as two distinctive taxa taking into account first the cytogenetic differences, chromosome number, and karyotypes, and second the distinctive germination mode of *Styphnolobium* and *Sophora* sect. *Calia* (Palomino et al. 1993).

The genus *Sophora* is a taxonomic group of pantropical distribution but with its center of diversity and an early Tertiary record in North America. Sousa and Rudd (1993) distinguished *Sophora* as perennials, shrubs, or trees without bracteoles and with a dehiscent legume, and *Calia* and *Styphnolobium* as trees with flowers with bracteoles and nondehiscent fruit. *Styphnolobium* differs from *Calia* in having leaves with stipels and legume with fleshy meso- and endocarp.

Styphnolobium affine (Torr. and A. Gray) Walp grows well in deciduous forests and grasslands. *Styphnolobium japonicum* is a deciduous tree endemic to China. *Sophora macrocarpa* is a characteristic endemic shrub from Chile that grows in open places or under the forest canopy. *Sophora prostrata,* a divaricate suckering shrub from New Zealand, grows well in grassland and rocky places. In contrast, the majority of the species of *Edwardsia* prefer lowland or lower mon-

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TABLE 1

NOMENCLATURE OF STUDIED SPECIES, INCLUDING SECTIONS

SPECIES NAME	SECTION
Sophora secundiflora Ortega ex DC.	*Calia*
Sophora chrysophylla (Salisb.) Seem.	*Edwardsia*
Sophora denudata Bory	*Edwardsia*
Sophora fernandeziana (Phil.) Skottb.	*Edwardsia*
Sophora howinsula (Oliv.) Green	*Edwardsia*
Sophora longicarinata G. Simpson & J. S. Thompson	*Edwardsia*
Sophora macnabiana (Grah.) Skottb.	*Edwardsia*
Sophora macrocarpa J. E. Sm.	*Edwardsia*
Sophora masafuerana (Phil.) Skottb.	*Edwardsia*
Sophora microphylla Ait.	*Edwardsia*
Sophora prostrata Buchan.	*Edwardsia*
Sophora tetraptera J. Mill.	*Edwardsia*
Sophora toromiro L.	*Edwardsia*
Sophora rhynchocarpa Griseb.	*Sophora*
Sophora linearifolia Griseb.	*Sophora*
Sophora tomentosa L.	*Sophora*
Styphnolobium japonicum (L.) Schott	*Styphnolobium*

tane areas along rivers and forest margins or outskirts. *Sophora longicarinata* (a recently reinstated species close to *S. microphylla*) is a shrub or tree of stressed habitats; it is known from the Takaka area of the northern South Island of New Zealand, restricted to marble or limestone sites (Heenan 1998). *Sophora denudata, S. chrysophylla,* and *Sophora* from Juan Fernández are found in uplands—*S. fernandeziana* appears on hills; *S. denudata,* a small tree from La Réunion, grows over *Acacia heterophylla* Willd. and is frequently associated with the ericaceous *Philippia montana* Klotsch.; similarly *S. chrysophylla* is the major tree in the treeline ecosystem on both Mauna Kea (Hawai'i) and Haleakalā (Maui) and is the successional replacer of *Metrosideros polymorpha* Gaud. (Mueller-Dombois 1987).

The first hypothesis put forth to explain the origin of *Edwardsia* suggests that their distribution center lies in the West Pacific with subsequent migration and differentiation from west to east, reaching South America, Hawai'i, Juan Fernández and Easter Islands, Gough Island in the Atlantic Ocean, and La Réunion in the Indian Ocean (Sykes and Godley 1968). Recently, Murray (1986) and Murray and Porter (1980) stated that *S. macrocarpa* is derived from *S. microphylla* of New Zealand on the basis of the similarity of the polypeptide and seed protein compositions of both taxa. It is surprising that those authors also recognized the strong similarity between these taxa and *Pisum sativum* in this regard, which seems to indicate that their method does not even discriminate at the suprageneric level. Similarly, Markham and Godley (1972) could not segregate the Chilean, Gough Island, or Chatham Island taxa from New Zealand material from both North and South Islands using their phenolic constituent patterns. Additional circumstantial evidence cited by Murray (1986) considered the hydrochoric character of *S. microphylla* seeds. Ramírez and Romero (1978) also observed the potential for hydrochoric seed dispersal in *S. macrocarpa.* There is no difficulty, however, in considering *S. macrocarpa* as the founding species of the section as a result of its possible relationship to American species in the section *Sophora* and because of its potential for hydrochoric seed dispersal. Two species from Argentina with a large, unwinged legume and dark brown seeds (cf. Burkart 1952), *S. linearifolia* and *S. rhynchocarpa,* restricted to Cordoba and San Luis Provinces, and to Salta Prov-

ince, respectively, are closest to Chilean *S. macrocarpa.* In the same vein, Skottsberg (1956) noted that the Chilean insular taxa, *S. fernandeziana, S. masafuerana,* and *S. toromiro,* are related and might be united in *S. tetraptera.* In the Juan Fernández Islands there is a high degree of endemism, and the principal source of its flowering plants is the continental flora of South America, representing about 47% (Hoffmann and Marticorena 1987).

The link between sections *Sophora* and *Edwardsia* is *S. macrocarpa.* In *Edwardsia,* the change in flower morphology can be related to the presence of a new pollination vector. *Calia, Sophora,* and *Styphnolobium* have an erect flag and are melittophylic, but *Edwardsia* has an extended one and is visited by birds. Such a change has been demonstrated in *Harpalyce* (Galegeae-Brongniartieae), whose resupinate flowers are inadequate to ensure successful pollination by bees (Arroyo 1976). Drepanididae visit *Sophora chrysophylla* in Hawai'i and the trochilid *Patagona gigas* visits *S. macrocarpa* in Chile (Arroyo 1981); other hummingbirds pollinate *S. tetraptera* and *S. microphylla* in New Zealand. It is interesting that the nectar of the ornithophilous *S. microphylla* kills bees, but is apparently not harmful to birds (Arroyo 1981).

Flowering plants were present in New Zealand by the Cenomanian, some 100 million yr B.P. (before the present) when it was in direct contact with Australia, New Caledonia, Antarctica, India, and South America (Raven 1973). Nevertheless, there is no palynological evidence for the existence of *Sophora* before Quaternary times (Mindelhall 1980). That there are only two species of *Sophora* in Australia, *S. fraseri* Benth. and *S. tomentosa* subsp. *australis* Yakovl., both from Queensland (fide Yakovlev 1967), suggests that it is a recent immigrant. All the volcanic islands of the Pacific Ocean appear to be at most a few million years old. In the Hawaiian Islands, Kaua'i is dated about 4.4–5.7 million yr B.P. and Hawai'i between 0.1 and 0.45 million yr B.P. (Macdonald et al. 1983). Juan Fernández Masatierra Island has been dated to between 3.7 and 4.3 million yr B.P. and Masafuera between 1.0 and 2.4 million yr B.P. (Stuessy et al. 1984). Lava from the Poike crater of Easter Island is 2.5 million yr old (Zizka 1988). Thus, an American origin for this section becomes an attractive alternative contrasting with the Gondwanic origin suggested for the *Edwardsia* species, as may deduced from Sykes and Godley's (1968) and Murray's (1986) reasoning (M. Kalin Arroyo, pers. comm.).

We have incorporated Lavin and Luckow's hypothesis in our model, because *Sophora* is a taxonomic group that meets the following three criteria: a center of diversity in North America, an early Tertiary fossil record in North America, and a pantropical distribution (Lavin and Luckow 1993). *Styphnolobium, Sophora,* and *Calia* are representatives of *Sophora* s.l. in the United States, suggesting migration of the latter from the Northern Hemisphere to South America. Another two cases demonstrated in the Papilionaceae are *Robinia* (Lavin and Luckow 1993) and the Psoraleeae (Grimes 1990). The fossil record of *Styphnolobium* is present in Middle Eocene deposits in North America (Sousa and Rudd 1993).

Both palynological and chemical evidence might corroborate or weaken the hypothesis of a closer relationship between the *Sophora* taxa from Juan Fernández Islands and South American stock close to *S. macnabiana* (*S. microphylla* from South America) than with their previously postulated Antarcto-Pacific relatives.

No recent micromorphological studies are available, with the exception of a partial analysis of the cuticles of some *Sophora* species belonging to the section *Edwardsia* (Lobin and Barthlott 1988, Aldén and Zizka 1989), all of which are very similar. Many years earlier, Heusser (1971) had described the pollen grains of the continental *Edwardsia* species as tricolporate, subprolate, with a suprareticulated exine 1 μm thick. Peña et al. (1993) studied the architecture of pollen of various *Edwardsia* compared with *Styphnolobium.*

The aim of this work was to put forth an alternate hypothesis to explain the origin of *Edwardsia* by using comparative chemistry

TABLE 2

DATA MATRIX FOR *Styphnolobium, Calia,* AND THE *Sophora* SPECIES STUDIED; 9 INDICATES INDETERMINATE OR INAPPLICABLE CHARACTERS

TAXON[a]					
STYPH	1 0 0 0 2	0 0 0 0 0	0 0 1 0 0	0 0 0 0 0	0 000
CALIA	1 0 0 0 0	0 0 0 0 0	3 0 0 0 0	1 0 0 0 2	0 191
TOMEN	0 0 0 0 0	0 0 0 0 1	0 1 0 0 9	1 1 2 1 0	1 110
LINEA	0 1 0 0 0	0 0 0 0 0	0 0 0 0 0	1 0 0 0 2	0 000
RHYNC	0 1 1 0 0	0 0 0 0 0	0 0 1 0 9	1 9 9 9 9	9 000
MACRO	0 0 0 0 0	1 0 1 0 0	0 0 0 0 1	1 0 0 2 2	0 001
CHRYS	1 1 0 0 0	1 1 1 1 1	2 1 1 1 1	1 0 0 2 2	1 111
DENUD	1 0 1 0 0	1 1 1 1 1	0 0 0 1 1	1 0 1 2 1	1 011
MACNA	1 1 1 1 1	0 1 1 1 1	1 1 1 1 1	1 0 2 2 0	0 011
FERN	1 0 1 0 1	1 0 1 0 1	0 0 0 0 1	1 1 0 2 2	1 101
MASAF	1 0 1 1 1	1 0 1 0 1	0 1 1 0 1	1 9 9 9 9	9 011
TORO	1 0 1 0 1	1 1 1 1 1	1 1 1 1 1	1 1 2 2 0	1 001
HOW	1 0 0 0 1	1 1 1 0 1	1 1 1 1 1	9 9 9 9 9	9 091
TETRA	1 1 0 0 0	1 2 1 0 1	1 1 1 1 1	1 0 2 2 0	0 011
MICRO	1 1 1 1 1	1 1 1 1 1	1 1 1 1 1	1 1 2 2 0	1 011
PROST	0 0 1 1 1	1 0 1 1 1	0 0 1 1 0	1 0 0 2 2	0 091

[a]STYPH, *Styphnolobium;* TOMEN, *Sophora tomentosa;* LINEA, *S. linearifolia;* RHYNC, *S. rhynchocarpa;* MACRO, *S. macrocarpa;* CHRYS, *S. chrysophylla;* DENUD, *S. denudata;* MACNA, *S. macnabiana;* FERN, *S. fernandeziana;* MASAF, *S. masafuerana;* TORO, *S. toromiro;* HOW, *S. howinsula;* TETRA, *S. tetraptera;* MICRO, *S. microphylla;* PROST, *S. prostrata.*

and morphological and palynological evidence.

MATERIALS AND METHODS

The exines of pollen grains of *Sophora* species were examined by scanning electron microscopy. The pollen grains were metallized with a gold-palladium layer 30–40 nm thick and then photographed with an Autoscan Siemens microscope according to the method of Lynch and Webster (1975). Pollen measurements were determined from low-resolution micrographs and exine ornamentation was described from plates taken at 10,000 × magnification. The scanty herbarium materials do not allow the assignment of mean or modal values: only measurement ranges are provided for pollen besides the ornamentation of exine.

Alkaloid extraction and GLC analysis have been described and discussed in a previous paper (Peña and Cassels 1996).

The characters were polarized by the out-group technique and processed by multiple most parsimonious trees option (mhennig*) with global branch swapping (bb*), implicit enumeration search option (ie*) with non-additive characters, and nelsen option (nelsen*) for consensus resolutions of Hennig86 (Farris 1988). Character states are shown in Appendix 1. Indeterminate characters coded as 9 in Table 2 were processed as 0 (synapomorphic).

The selection of an operative out-group for *Edwardsia* lies in other sections of *Sophora,* mainly Calia and the genus *Styphnolobium.* Many characters show that these two genera are closely related. A number of characteristics of *Styphnolobium* Schott. allow it to be considered as an out-group of *Sophora:* the presence of stipulae, of reserve albumen in the seeds, the distinctive chromosome number ($n = 14$), the presence of seed galactomannans, hypogeal germination, and the heterobrochate exine (Bailey 1974, Goldblatt 1981, Polhill 1981, Peña et al. 1993) (Table 2). Both *Calia* and *Edwardsia* have cotyledons with epigeal germination, contrasting with sections *Styphnolobium* and *Sophora* in which germination is hypogeal.

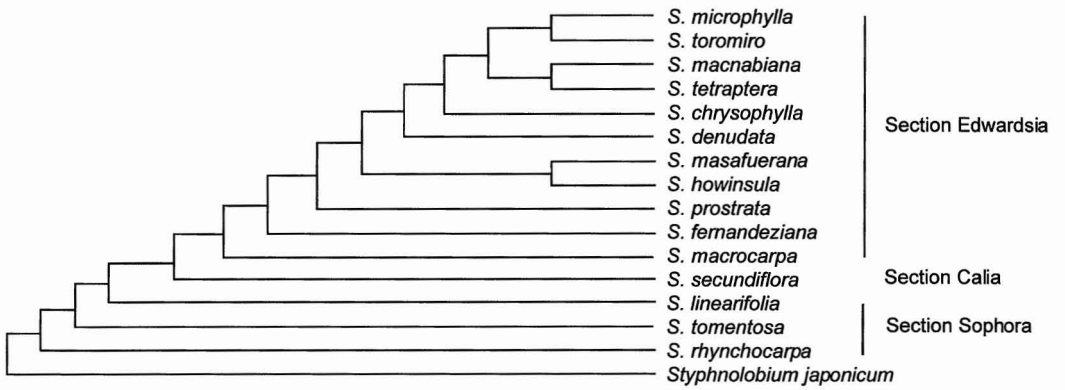

FIGURE 1. Cladogram of *Sophora* sect. *Edwardsia,* using 22 characters: 1–16, morphology; 17–23, chemistry; 23, palynology; and 24, germination.

RESULTS

Incomplete data used in previous studies did not allow a hypothesis to be elaborated to explain the origin and evolution of *Sophora* species, especially for section *Edwardsia.* We have now been able to reconcile geological, palynological, morphological, germination, and chemical evidence related to Chilean mainland and oceanic island (5 species) material and from another collection of *Edwardsia* (La Réunion [1], New Zealand [4], and Hawai'i [1]).

The cladogram of *Sophora* sect. *Edwardsia* group (Figure 1) is one of the 43 most parsimonious cladograms generated by Hennig86 using multiple most parsimonious trees option (mhennig*) with global swapping (bb*). The cladogram has 84 steps, a consistency index of 0.36, and a retention index of 0.60. The relationships discussed below are those consistently resolved in 25 cladograms. Implicit enumeration search option (ie*) with all characters nonadditive gives similar results. The other 16 cladograms are variants of the one presented and have no bearing on a discussion of the origin of the *Edwardsia* group. Only four represent a nonmonophyletic arrangement of sect. *Edwardsia,* partly due to chemical homoplasious characters; therefore *S. tomentosa* sometimes converges with the more advanced *Edwardsia.*

The cladogram represents the relationships that were consistently resolved in five trees, depicted in Figure 1. *Edwardsia* is monophyletic by 6, 8, 15, and 19. *Sophora microphylla, S. toromiro, S. tetraptera, macnabiana, S. masafuerana,* and *S. howinsula* are sister groups. *Calia* (*S. secundiflora*) appears as a paraphyletic assemblage of *Sophora* sect. *Edwardsia.* Both *Calia* and *Edwardsia* have cotyledons with epigeal germination, contrasting with sections *Styphnolobium* and *Sophora* in which germination is hypogeal. Here this condition is viewed as symplesiomorphic. Otherwise, three resolutions from 19 remnant trees show four polyphyletic trees for sections of *Sophora,* and five gave *S. prostrata,* a species with many symplesiomorphic characters, near the base of the *Edwardsia* group. In three cases linkage of *S. tetraptera* with *S. denudata* and *S. chrysophylla* was found; these tree species are considered closely allied by many specialists (Green 1970).

The following chemical compound characters are informative: replacement of tetra- by tricyclic quinolizidine alkaloids in *Calia* [sect. *Calia* (Berland) Rudd.], which has a high cytisine content, like *Edwardsia,* in contrast with section *Sophora,* which has a higher sparteine content. Hoeneisen et al. (1993) isolated formylcytisine from two Chilean species, *S. fernandeziana* and *S. macnabiana.* This is probably the only chemical linkage found between these two species

to the apparent exclusion of others, although it seems only to represent an intermediate biosynthetic step between methylcytisine and cytisine, common to all *Edwardsia.* Markham and Godley (1972) merged *S. macnabiana* (Chile) with *S. microphylla* (New Zealand) populations because of the similarity of the leaf flavonoid patterns. Our chemical results with the seed alkaloids contradict a relationship between these species, particularly considering the methylcytisine/cytisine ratio: a New Zealand population preferentially accumulates the methyl derivative, whereas Chilean populations contain higher proportions of the nonmethylated compound.

Sophora denudata and *S. chrysophylla* show some similarities in their morphological (1, 6–10, 14–16), palynological (23), germination (24), and some chemical (19, 21) characters. *Sophora microphylla* and *S. macnabiana* show many synapomorphic characters (1–5, 7–16, 18–19, 23–24). *Sophora toromiro* only differs in ornamentation of the exine (23), two chemical characters (17 and 21), and three morphological characters (2, 4, and 6). Chemically, these two species may be linked with *S. tetraptera* and *S. macnabiana* by cytisine and sparteine contents (18, 19).

The relationship between *S. masafuerana* and *S. howinsula* deserves further comment. Many indeterminate characters here were coded as 0 or symplesiomorphic, 17–21. In addition, characters 16 and 23 in *S. howinsula* make this relationship dubious.

DISCUSSION

We previously proposed a South American origin for section *Edwardsia* of *Sophora* (Peña et al. 1993) based upon palynological and chemical data. Many lines of evidence were not congruent with a New Zealand center of origin for *Edwardsia* as a whole. We later confirmed (Peña and Cassels 1996) this hypothesis by incorporating phytochemical evidence. Although the chemical characters are poor discriminators, they do not falsify our proposal of a South American primary center of diversification and ultramarine migration to the Pacific and Indian oceanic islands.

The Papilionaceae are usually discussed as of Gondwanic origin, because their major diversity is in tropical Africa and South America (Raven 1973, Kamp 1980, Raven and Polhill 1981). In this vein, it is assumed that North American tropical representatives evolved from South American ancestors (Taylor 1990).

Sophora macnabiana, a Chilean species close to *S. microphylla* and putatively derived from it, represents the most advanced taxon in section *Edwardsia. Sophora fernandeziana* and *S. macrocarpa* share ancestral, morphological, chemical, or palynological characters. Considering the flora of the Juan Fernández Islands, *S. fernandeziana* appears closely related to *S. macrocarpa* (6–8, 15, 16, 19, 20, and 24), but parallel evolution seems to be the simplest explanation. Similarly, *S. masafuerana* appears closer to the *microphylla* group. The palynological characters of the former two, *S. fernandeziana* and *S. macrocarpa* (exine heterobrochate), contrast with the homobrochate exine of *S. masafuerana, S. macnabiana,* and most insular *Edwardsia* species (Peña et al. 1993). Therefore, derivation of the insular species, particularly of *S. fernandeziana,* from continental species cannot be dismissed. *Sophora macrocarpa* and *S. fernandeziana* share a number of characters (15, 19, and 20: absence of auricles on the petals, percentage of matrine, and methylcytisine/cytisine ratio). The relationship of *S. toromiro* remains unclear: chemistry characters coincide with *S. microphylla* but palynologically it is close to the South American group, with exine heterobrochate.

CONCLUSIONS

Consistent with the Boreotropic hypothesis, a primary diversification center in South America and subsequent migration to the Indian Ocean, New Zealand, the Juan Fernández Islands, Easter Island, and possibly the Hawaiian Islands is the simplest explanation for the evolution of *Edwardsia* species

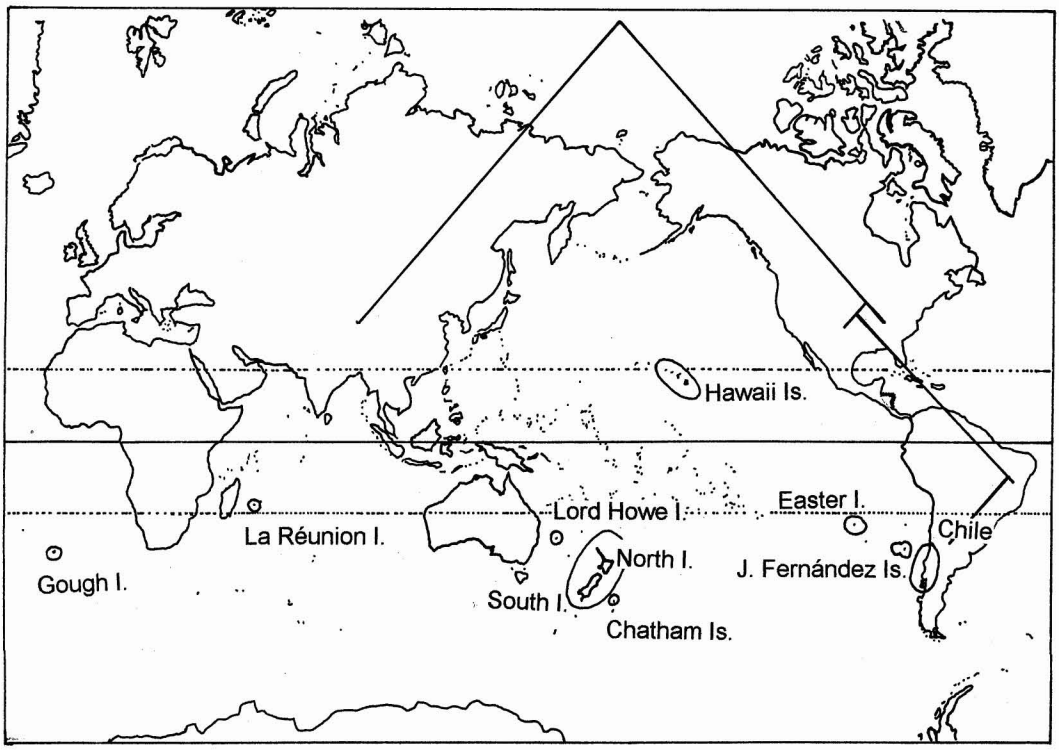

FIGURE 2. Area cladogram of some representatives of *Sophora* depicting South American elements ultimately derived from North American lineages *Styphnolobium* and *Calia*.

(two mainland and nine ultramarine) taking into account comparative morphological, palynological, and chemical evidence (Figure 2).

Our results are consistent with Lavin and Luckow's (1993) hypothesis. First, *Sophora* is a taxonomic group that meets the following three criteria: a center of diversity in North America, an early Tertiary fossil record in North America, and a pantropical distribution. *Styphnolobium, Sophora,* and *Calia* are representatives of *Sophora* s.l. in the United States, suggesting migration of the latter from the Northern Hemisphere to South America. *Styphnolobium* is present in Middle Eocene deposits (Sousa and Rudd 1993). On phylogenetic grounds, the mainland Chilean species of *Sophora* appear to have been derived from ancestors near the extant Argentinean species *S. linearifolia* and *S. rhyncho-carpa* and the psammophyte *S. tomentosa* growing at tropical coastal sites around the world.

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APPENDIX 1
CHARACTER STATES: CODING NUMBERS, CHARACTERS, AND STATES

1: Life form: shrub, 0; tree, 1.
2: Number of leaflets: few, 0; 15–25, 1.
3: Length of leaflets: over 1 cm, 0; less than 1 cm, 1.
4: Length/width of leaflets ratio: more than 2, 0; less than 2, 1.
5: Pubescence of the leaflets: face and back, 0; back only, 1.
6: Direction of flag: erect, 0; extended, 1.
7: Flag/wings ratio: same, 0; much longer, 1 and 2.
8: Exertion of stamens: no, 0; yes, 1.
9: Strangulation of the lomentum: no, 0; yes, 1.
10: Length of seed: large (1 cm or more), 0; small, 1.
11: Seed color: brown, 0; ocher, 1; orange, 2; reddish, 3.
12: Number of seeds per fruit: few (2–5), 0; 6 or more, 1.
13: Pubescence of the lomentum: marked, 0; slight, 1.
14: Presence of wings on the fruit: yes, 1; no, 0.
15: Presence of auricules on the petals: yes, 0; no, 1.
16: Presence of stipulae: yes, 0; no, 1.
17: Methylcytisine percentage: below 30%, 0; over 30%, 1.
18: Cytisine percentage: below 31%, 0; over 31%, 1.
19: Sparteine percentage: none detected, 2; below 1%, 1; over 1%, 0.
20: Matrine percentage: below 31%, 1; over 31%, 0.
21: Methylcytisine/cytisine ratio: less than 0.5, 0; more than 0.5, 1.
22: Anagirine percentage: below 1%, 1; over 1%, 0.
23: Exine ornamentation: heterobrochate, 0; homobrochate, 1.
24: Germination: epigeal, 1; hypogeal, 0.